# Effects of damselfish territorial defense on species composition and spatial structure of mixed species schools

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*Abstract:* Fishes form mixed species schools for two primary reasons: predator avoidance and feeding enhancement. By grouping in schools, fish are able to penetrate damselfish territories and gain access to defended resources. In this study, we explore the tendency of fish to school, species composition, and spatial structure of schools in areas of high and low damselfish density. We predicted that in areas of high damselfish density 1) there would be a higher percent of fish schooling, 2) schools would have a higher species diversity and a greater proportion of herbivores, and 3) schools would have a greater number of individuals or be smaller in area, and therefore have a greater fish density. We suggest that the benefit of access to damselfish territory, provided by schooling in areas of high damselfish density, may explain the greater likelihood of fish to school and the higher species diversity within schools. We also suggest that the greater tendency of invertebrate feeders to school in areas of high damselfish density is due to increased access through schooling to invertebrate prey associated with the defended algal mats. Finally, our results suggest that increasing density of fish in schools may be a more effective means of gaining access to defended territories than increasing the absolute number of fish in schools.

*Key Words: coral reef fish, diversity, foraging guild, predator avoidance*

## Introduction

Many coral reef fishes exhibit both solitary and schooling behavior. There are two most widely accepted explanations for schooling (Foster 1985). First, schooling aids in predator avoidance, allowing fish to detect predators earlier, potentially confuse predators by making it difficult for the predators to choose one fish to attack, and by decreasing the probability that one fish is attacked (see references in Foster 1985). Second, there are feeding benefits associated with schooling that include increased time for foraging due to reduced time spent being vigilant for predators (Pitcher and Magurran 1983, as cited in Foster 1985), decreased time searching for food patches (Pitcher et al. 1982, as cited in Foster 1985), and the ability to overwhelm territorial defenders of food patches (see references in Foster 1985). The relative benefits of predator avoidance or feeding enhancement may differ in different habitats. For example, Foster (1985) demonstrated that the greatest benefits of schooling were a result of increased food availability after overcoming territorial damselfish, and not from decreased time watching for predators (Foster 1985).

In this study, we explore 1) the tendency of fish to school, 2) species composition and 3) spatial structure of schools in areas of high and low damselfish abundance. Since overwhelming damselfish territories to gain access to their algal mats may provide a strong incentive to school, we predict that schools will contain both more individuals and more species of fish in areas of high damselfish density than in areas of low density. Further, we predict that these schools will have a greater proportion of herbivorous feeders than schools in areas with low damselfish density since algal mats are not defended. Finally, if greater density facilitates more successful invasion of damselfish territories, we expect that schools in areas of high damselfish density will have a greater number of individuals or be smaller in area, and therefore have a greater fish density than schools in areas of low damselfish density.





## Methods

This study was conducted in the west fore reef of Discovery Bay, Jamaica, West Indies on 4 - 9 March 2000 between 8:45 and 12:45 daily. Data were collected by SCUBA diving at the Long Term Study Site, Mooring 1, and Dancing Lady moorings in areas with low and high densities of damselfish territories (damselfish > 4 and < 2 m apart, respectively). The actual damselfish densities were found to be 2.96 territories/10m$^2$ for high density and 0.47 territories / 10 m$^2$ for low density areas. To determine the structure and species composition of schools, we haphazardly selected six mixed species schools in both areas of low and high densities of damselfish territories at each site. We defined a mixed species school as a group of three or more individual fish with at least two different species that were traveling or foraging together. Since schools appeared to be generally two-dimensional in shape (spread out flat with fish foraging on the bottom), we described school composition and structure by observing schools from above. We defined two positions within the two-dimensional school. The center was the area of the smallest circle to encompass all clustered individuals that were within one body length of their nearest neighbor. The periphery was the area beyond the center and included all peripheral individuals associated with the school. We estimated the diameter (m) of the school and the center, and recorded the number of individuals of each species occupying central and peripheral positions three times at three min intervals. These observations were then averaged for each school and schools served as independent replicates. Schools were not included in analyses if the school disbanded during the nine min of observation or if schools in low damselfish density areas interacted with defending damselfish.

To determine the likelihood of fish species to exhibit schooling and solitary behaviors, we swam 20 m long by 2 m wide transects in both low and high damselfish density areas, recording the number of individuals of a species that were seen schooling and solitary in both low and high damselfish density areas ($n = 18$ and $n = 18$, respectively).

To determine differences in school behavior both within and between areas of high and low damselfish density, we used a two-way ANOVA model with main effects of school behavior and damselfish density, and fish abundance as the response variable. Similarly, we used a two-way ANOVA with main effects of feeding guild and damselfish density, and proportion of fish in each school (arcsine transformed) as the response variable. We used Student's t-test to compare the mean Shannon diversity index of schools between high and low damselfish density areas. For each species, we compared the abundance of fish schooling in high and low damselfish density areas, and occupying the central and periphery positions within a school (Student's t-test). Since we analyzed each species with an individual Student's t-test, there is a high probability of type I error in this analysis. We calculated the mean area of a school ($\pi$ * (diameter of periphery/2)$^2$) and center of the school ($\pi$ * (diameter of center/2)$^2$; $n = 3$ observations). We then compared the abundance of fish within and the area of the entire school and only the center of schools between in high and low damselfish density areas (Student's t-test).

## Results

There was a significant effect of the interaction between damselfish density and schooling behavior on the number of fish in each transect (Fig. 1; $F_{1,57} = 20.72$, $p < 0.001$). The results of the orthogonal contrasts for this interaction indicate that the likelihood of a fish to school was higher in high damselfish density areas than in low damselfish density areas ($p < 0.001$), and in high damselfish density areas more fish were seen in schools than solitary ($p < 0.001$), while in low density areas the proportions were not different ($p = 0.78$).

Mixed species schools were more diverse (Shannon Diversity index ± SE) in areas of high damselfish density than in low density ($H' = 1.43 \pm 0.07$ and $1.18 \pm 0.07$, respectively; $t = 2.70$, $df = 34$, $p = 0.01$). Barred Hamlet was the only fish of 13 schooling species found in greater abundances in schools in high than low damselfish density areas (Fig. 2; $t = 2.33$, $df = 39$ $p = 0.031$). There was a significant interaction between feeding guild and damselfish density ($F_{1,67} = 33.39$, $p < 0.001$).

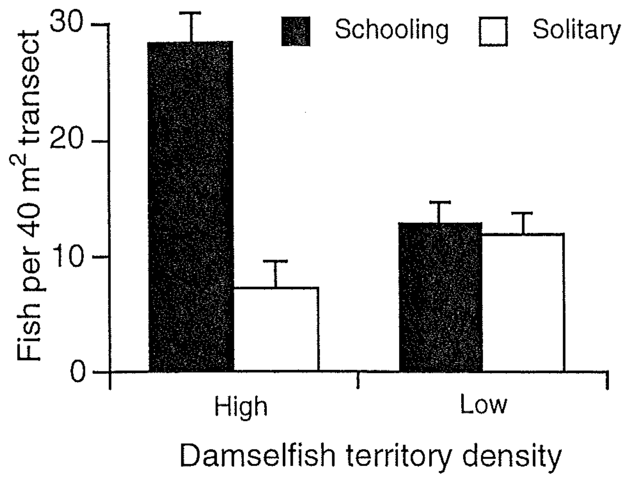


Figure 1. Mean schooling and solitary fish observed per 40 m$^2$ transect in high and low damselfish density areas in Discovery Bay, Jamaica (n = 59 transects).

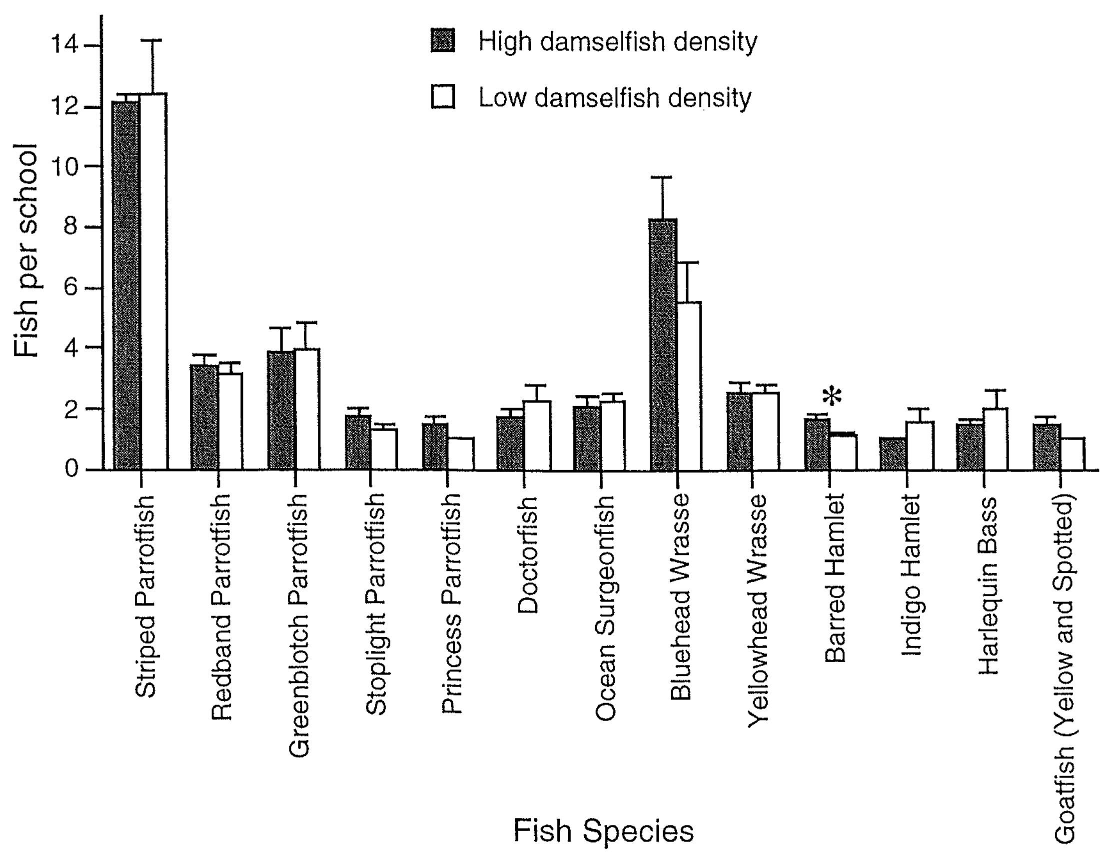


Figure 2. Mean abundance of schooling species in areas of high and low damselfish density in the fore reef of Discovery Bay, Jamaica (n = 18 and 18 schools, respecitively). (* means are significantly different, P < 0.05).





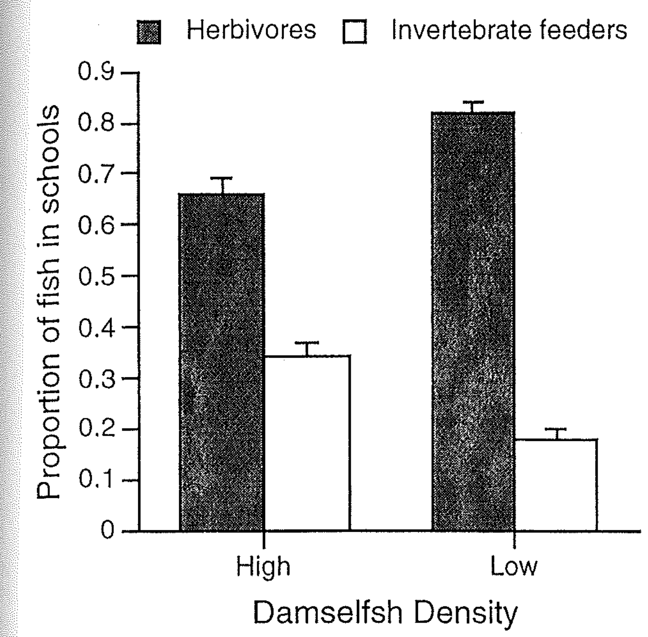


Figure 3. Proportion of herbivores and invertebrate feeders represented in schools found in low and high damselfish density areas (n = 18 and 18, respectively) in the fore reef of Discovery Bay, Jamaical, West Indies.

The results of orthogonal contrasts for this interaction indicate that herbivores represented a higher proportion of schooling fish than invertebrate feeders, and herbivores made up a higher proportion of schooling fish in areas of low damselfish density than in areas of high damselfish density, while invertebrate feeders made up a higher proportion in high than in low damselfish density areas (p values < 0.05).

Mean abundance of fish per transect (± SE) was marginally higher in areas of high damselfish density than in areas of low damselfish density ($31.81 \pm 4.50$, $22.29 \pm 2.16$, respectively; $t = 1.94$, $df = 31$, $p = 0.061$). However, the mean number of fish within a school was not significantly different between high and low damselfish density areas (Fig. 4a; $t = 0.96$, $df = 26$, $p = 0.35$). The mean area of a school was smaller in high damselfish density areas (Fig. 4c; $t = -4.46$, $df = 26$, $p = 0.001$), therefore the mean density of fish within a school (± SE) was greater in areas of high damselfish density than in areas of low damselfish density ($13.09 \pm 1.64$ and $4.47 \pm 0.99$, respectively). Similarly, the mean number of fish occupying central positions within a school was not significantly different between high and low damselfish density areas (Fig. 4b; $t = 1.18$, $df = 26$, $p = 0.25$), while the mean area of the center was marginally smaller (Fig.4d; $t = -1.80$, $df = 26$, $p = 0.08$). Thus, the mean density of fish within the center (± SE) was greater in areas of high damselfish density than in areas of low damselfish density ($68.41 \pm 10.8$ and $20.35 \pm 3.09$, respectively). Of the 13 species of schooling fish, only striped parrotfish, redband parrotfish, greenblotch parrotfish, and bluehead wrasse were more likely to be in the center than in the periphery of a school (Fig. 5; $t = 6.79$, $df = 68$, $p < 0.001$; $t = 2.22$, $df = 61$, $p = 0.03$; $t = 2.03$, $df = 23$, $p = 0.05$; and $t = 3.90$, $df = 35$, $p < 0.001$, respectively).

## Discussion

Enhanced feeding opportunities may explain the greater likelihood of fish to school, the higher species diversity within schools, and the spatial structure of schools in areas of high damselfish density. The greater diversity in schools in areas of high damselfish density than in areas of low damselfish density resulted not from the addition of more herbivorous fish species, as we predicted, but from the addition of invertebrate feeders. This, along with the higher numbers of invertebrate feeders schooling in areas of high damselfish density, suggests that schooling may provide increased access to invertebrate prey in addition to algal resources. Erect algae such as *Sargassum*, which is often more abundant in areas defended by damselfish, can provide refuge for small invertebrates (McClanahan et al. 1999 and references therein) such that areas of high algal density also have high invertebrate density (Ogden 1976). Wrasses may also take advantage of the increased foraging activity of herbivores in schools in dam-

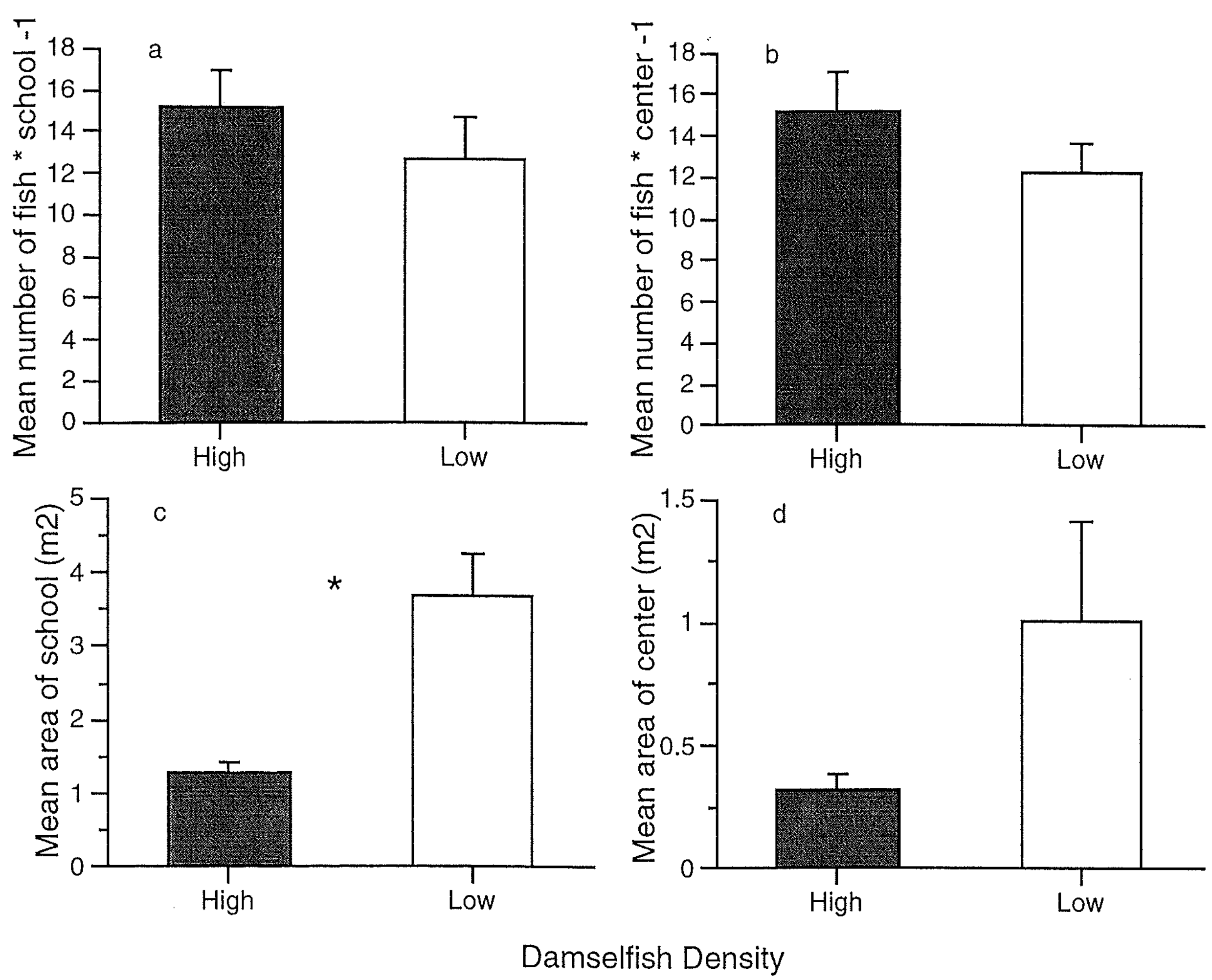


Figure 4. Mean number of fish a) in a school and b) in the center of a school, and mean area c) of a school and d) of the center of a school, in high and low damselfish density areas ( n = 15 and 13 schools, respectively), in the fore reef of Discovery Bay, Jamaica, West Indies (* means are significanly different, P values < 0.05).

selfish territories, which may stir up invertebrate prey into the water column to increase prey acquisition (Barlow 1974). Finally, greater ambient concentrations of nutrients, such as nitrogen and phosphorous, derived from fish excretion in areas of high damselfish density may result in richer substratum for invertebrates (Klumpp et al. 1987). Furthermore, it has been shown that when given access to defended algal mats, some benthic invertebrate feeders will shift their foraging preference from plankton to algae (Foster 1985). Future studies could investigate the potential of such shifts in foraging habitat by invertebrate feeders in schools.

Although previous research on spatial structure suggests that large groups of fish are more effective at gaining access to territories defended by damselfish (Foster 1985 and references therein), our results suggest that increasing school density may actually be a more effective strategy than increasing numbers of fish. Schools in areas of high damselfish abundance were no larger than those is areas of low damselfish abundance, but did have a higher density of fish per unit area. This higher density may be an effective way to overwhelm damselfish. In contrast, increasing school size may not be to gain access to damselfish territory and may result in lower





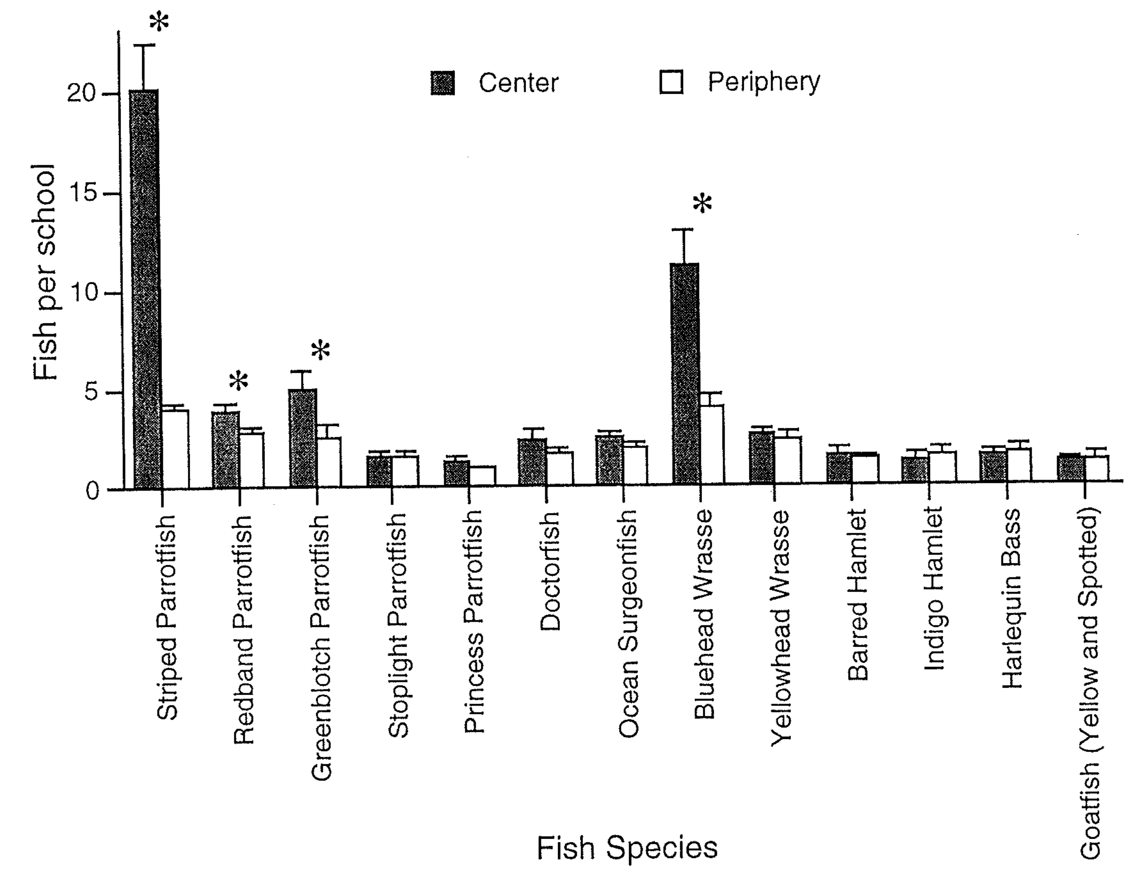


Figure 5. Mean abundance of schooling species in the center and periphery of schools in the fore reef of Discovery Bay, Jamaica (n = 18 and 18 schools, respecitively). (* means are significantly different, P < 0.05).

energy returns per fish. The greater likelihood of striped parrotfish, redband parrotfish, greenblotch parrotfish, and bluehead wrasse to be found in the center rather than the periphery of a school suggests that they may initiate the attack on damselfish territories, perhaps benefiting most from invasion of the territories, and therefore be more permanent school members or leaders.

In summary, our results suggest that as a result of different advantages of schooling in areas of high damselfish density, school composition and spatial structure can greatly vary: in areas of high damselfish density, schooling is more likely, schools are more dense, and schools are more diverse due to the addition of invertebrate feeding fishes. Schooling appears to be a complex, multifunctional behavior which can vary greatly across a multitude of coral reef habitats.

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